Revista Chilena de Historia Natural
67: 177 - 182, 1994

Effect of fire on plant architecture in Chilean shrubs

Efecto del fuego sobre la arquitectura de plantas en arbustos chilenos

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ABSTRACT

Plant architecture is the result of meristem activities, genetically determined but triggered by environmental factors. Changes in the architecture may arise due to the effect of certain factors that remove biomass such as fires and herbivores. In this work we analyze metameric modifications arising from the effect of fire in the architecture of four dominant shrubs of the mediterranean zone of central Chile. The analysis of plant regeneration after fire shows that there is no variation as regards types of modules developed in each species. A change in the proportions of the developed modules and their spatial arrangement were observed in plants recovering after fire. Differences found between species are discussed in terms of their different growth habit.

Key words: Plant architecture, Modules, Fire, Matorral.

RESUMEN

La arquitectura vegetal resulta de la actividad de los meristemas la cual, aunque está genéticamente determinada, puede ser modificada por diversos factores ambientales. Como consecuencia de los efectos de algunos factores que remueven biomasa, tales como el fuego y la herbivoria, pueden generarse cambios en la arquitectura de una especie vegetal. En este trabajo se analizan las modificaciones morfológicas generadas por el efecto del fuego en la arquitectura de cuatro especies arbustivas dominantes del matorral de la zona central de Chile. El análisis de la regeneración de los arbustos después del incendio indicó que no existe variación en cuanto al tipo de módulos que cada especie es capaz de desarrollar. En plantas en regeneración después del incendio se observó un cambio en la proporción de los tipos modulares generados y en la disposición espacial de éstos. Las diferencias encontradas entre las especies se discuten en términos de sus distintos hábitos de crecimiento.

Palabras claves: Arquitectura vegetal, módulos, incendios, matorral.

INTRODUCTION

Plants can be considered as modular organisms, where the basic construction unit is repeated sequentially from one growth season to another. The spatial arrangement of these modules can be described as a metameric architecture. (White 1979). Most dominant shrubs in the Mediterranean zone of central Chile presented five types of modules originating from a terminal or anaxillary bud (Ginocchio & Montenegro 1992, Montenegro & Ginocchio1993). These modules or construction units correspond to: a) a flower or inflorescence, b) long shoots, c) temporal short shoots that may develop into a long shoot during the next growing season, d) a leafy short shoot with limited growth by the transformation of its apical meristem into a flower or in florescence, and e) a lignified short shoot that turns into a thorn. According to the position of renewal buds these modules may form seven different spatial arrangements, four of them found mainly in evergreen shrubs, two characteristic of summer deciduous species and one equally frequent in both growth forms (Ginocchio & Montenegro 1992, Montenegro & Ginocchio 1993).

Metameric architecture is the result of terminal and axillary meristem activity triggered by environmental factors, closely related to the phylogenetic history of each species. Changes in the metameric architecture of a given plant may arise due to

(Received 4 October 1993; accepted 28 March 1994)

proportional differences between the developed modules and their different spatial arrangements, as a result of physical environmental conditions such as temperature, light, water and nutrients, or the effects of certain factors that remove biomass such as herbivory and fire (Kuppers 1989, Ginocchio & Montenegro1993).

Anthropogenic fires occur frequently in Central Chile mainly during the drought season (Haltenhoff 1991). Most native species survive after fire due to their great regeneration capacity (Altieri & Rodríguez 1974, Araya & Avila 1981) from below ground epicormic buds and lignotubers (Montenegro et al. 1983, Montenegro& Teillier 1988), a large underground burl that acts as a storage organ which allows the plant to resprout quickly after fire. Observations in evergreen shrublands of other mediterranean regions of the world have shown that the degree of post-fire resprouting depends on the season of the year in which the fire occurs and also on the density of the branches forming the plant canopy before fire (Malanson & Trabaud 1988). Thus, the intensity and frequency of fire have a deleterious effect on resprouting potential (Kayll & Gimingham 1965). The importance of any of these factors may vary depending on their effect on the bud reservoir or bud bank responsible for the resprouting potential.

The most obvious change in shrub architecture due to fire is the adoption of a vertical structure brought about by the development of numerous long shoots arising from the soil surface (Araya & Avila 1981).

Since the plant must regenerate its photosynthetic leaf area to reestablish primary production, it is to be expected that most of the bud bank would be used for vegetative production rather than reproductive modules.

The purpose of this work is to describe the morphological modifications arising from the effect of fire in the metameric architecture of a plant, through the comparison of the amount of vegetative and reproductive modules developed and their spatial arrangement in two years after fire sites. Proportional modular differences due to microclimatic differences and water availability were also assesed analyzing shrubs located in both equatorial and polar facing slopes.

MATERIALS AND METHODS

Plant species

The species analyzed were the evergreens *Quillaja saponaria, Lithrea caustica* and *Cryptocarya alba*, and the summer deciduous *Trevoa trinervis*, all of them dominants in the matorral communities from sea level up to 1800 masl (Montenegro et al.1979, 1981).

The species studied have different growth patterns (Figure 1). *Q. saponaria* flowers appear at the end of the growing period and on terminal positions only, while long shoots are developed in axillary position at the beginning of the growth season.

L. caustica and *C. alba* begin activity by the development of flowers from axillary buds growing vegetatively, and after wards with the formation of apical and lateral long shoots. In *T.trinervis* reproductive modules are represented by short shoots bearing terminal and axillary flowers. Long shoots develop from the uppermost vegetative buds at the onset of the growth season (Ginocchio & Montenegro 1992, Montenegro & Ginocchio 1993).

Study site

The study area is near the Lo Orozco locality, in the Vth Region of the country (33°10'S - 71°22'W). The area has a mediterranean climate with coastal influences. Median annual precipitation is 588 mm, and the median yearly temperatures are 6.7 and 21.8 °C (Di Castri & Hajek 1976). The soil is granitic (Wright 1960).

Two slopes which burned during the summer of 1989 were chosen in this zone, one facing the pole and the other the equator. Their respective controls were two nearby slopes, undisturbed for the past ten years. Since some shrub species flower in branches developed during the previous growth season (Montenegro et al. 1988, 1989), burned sites in their second year of recovery were chosen.

In each of these four slopes, five *Q. saponaria* and *L. caustica* shrubs were selected. In addition, five *C. alba* shrubs were chosen in the polar facing slopes, and five *T. trinervis* shrubs in the equatorial slopes.

Five branches formed during the 1989 growth season were tagged in each shrub, and the total number of floral and vegetative modules developed during the 1990 growth season were counted. The tagged branches of the burnt shrubs corresponded to renewal shoots from the lignotuber. Observations were made during September and November 1990. During this short period, it was possible to distinguish betwen vegetative and floral buds, both in the evergreen and summer deciduous species (Montenegro et al. 1989).

In this work, long shoots or branches with long internodes were considered as vegetative modules; inflorescences and short shoots bearing inflorescences in *T. trinervis* were considered as reproductive modules.

Statistical Analysis

Mean reproductive and vegetative modules formed by woody species in control and burnt areas between polar and equatorial slopes and also inside each slope were compared using t-tests (Steel & Torrie 1985).

RESULTS

There was no variation on types of modules developed in each species, when compared to control shrubs. Instead a change was observed in the proportions of the developed modules and in the spatial arrangement of the module types in plants recovering after fire. The latter trend was present only in *T. trinervis* which developed numerous long shoots in the lower part of the branches while short shoots were formed in the upper part of the same branches. This architectural pattern is the opposite shown by control shrubs of the same species (see Figure 1).

As expected, the burnt shrubs produce a significantly larger number of vegetative

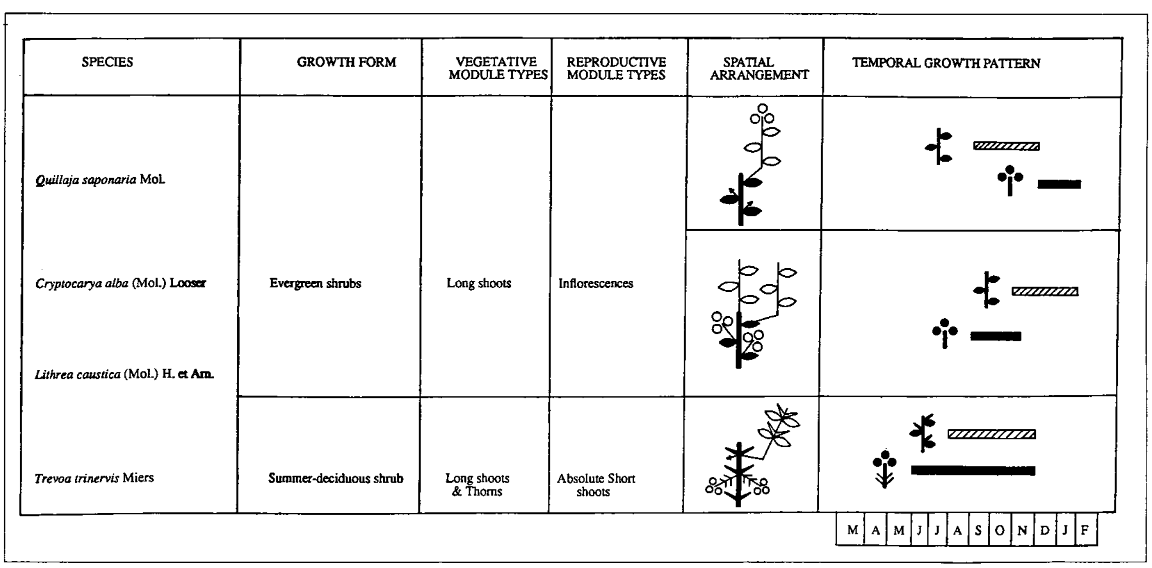

Fig. 1: Growth form, module types, spatial combination and temporal modular growth pattern in control shrubs of the four analyzed species. Growth period of vegetative and reproductive module types are shown in dashed and filled bars, respectively.

Forma de crecimiento, tipos modulares, disposición espacial y patrón temporal del crecimiento modular para un arbusto control tipo de las cuatro especies analizadas. Las barras achuradas indican el período de crecimiento de los módulos vegetativos, mientras que las barras oscuras indican el período de crecimiento de los módulos reproductivos.

modules (Table 1 and 2), as compared with shrubs not affected by fire (t test, $p<0.05$). Only *T. trinervis* shrubs formed reproductive modules as early as the second year after fire (Table 2). The amount of reproductive modules was similar for control and burnt sites, while a significant increase in vegetative modules was obtained in the burnt sites. Unburnt evergreen shrubs growing in polar facing slopes developed reproductive modules (Table 1).

The facing of the slope appears not to be important in terms of the number of vegetative modules developed by *Q. saponaria* shrubs (t test, $p<0.05$). However, in shrubs of *L. caustica* resprouting after fire differences were found between those growing in equatorial and polar slopes (Table 1 and 2); the latter developed a larger number of vegetative modules (t test, $p<0.01$).

DISCUSSION

The most evident architectural change after fire was due to variations in the proportion of modules produced. Shrubs of the four species analyzed resprouted producing a larger number of vegetative modules by branch. With the exception of *T. trinervis,* this increase in the production of long shoots was due to the development of axillary buds located in the most basal position of the branches, buds that were observed to remain dormant in control shrubs. Similar results have been found when comparingt he increase in foliar area of individuals previously felled (Montenegro et al. 1983).

Only *T. trinervis* shrubs showed an additional change in spatial distribution of vegetative as well as reproductive modules. The absolute short shoots were concentrated in apical positions, while long shoots were found in basal positions of each branch. In control shrubs the spatial distribution patterns was exactly the opposite. Hoffmann (1972), studying the first stages of development in seedlings of this species, describe that long shoots were formed from the base of the plant and that only after the second year of growth some long shoots were formed in the apical position. From this information, it could be deduced that this change in modular disposition would have a genetic basis.

The modifications described in the proportion of modules as well as in their spatial distribution, plus to the differences observed in foliar morphology, such as a larger area in burnt shrubs, indicate that fire, when destroying aerial biomass, would bring about a «rejuvenation» of the shrubs.

Plants require a minimum level of vegetative production before starting the reproductive processes (Hillman 1962). The speed with which this initial level is reached depends on the growth pattern and life history of the species. For the species analyzed, summer deciduous shrubs, such

TABLE 1

Mean reproductive and vegetative modules formed in shrubs located in recently burned polar slopes and in polar slopes wich were relatibely undisturbed during the last ten years. Standard desviation is shown in brackets.

Promedio de los módulos vegetativos y reproductivos formados en arbustos ubicados en laderas polares recientemente incendiadas y en laderas polares relativamente poco perturbadas desde hace diez años. Entre paréntesis se indican las desviaciones stándard.

Analyzed species	Burnt slope Vegetative modules	Burnt slope Reproductive modules	Control slope Vegetative modules	Control slope Reproductive modules
C. alba	54.6 (4.13)	0	2.6(1.69)	6.4(3.35)
L. caustica	58.8(12.01)	0	15.6(6.01)	0.4(2.44)
Q. saponaria	42.4(14.91)	0	10.4(2.46)	1.6(1.60)

as *T. trinervis*, show a different phenomor phology as compared with evergreen shrubs. Summer deciduous species begin the growing season after the first rains of the year and continue to grow for six months, while evergreen species have a three month growing season (Kummerow etal. 1981). In terms of the overall carbon balance it has been shown that summer deciduous leaf photosynthetic rates are greater than the ones in evergreen (Oechel et al. 1981), and the cost of growing leaves lower than in evergreens (Miller 1981, Merino 1987). So the time needed to recover the growth cost of leaves and its associate shoots is smaller in summer deciduous shrubs (Miller 1981). Growth and maintenance costs of evergreen leaves are higher than in deciduous leaves so reproductive processes could be delayed. This is shown both in control and burnt areas.

If there really is a minimum vegetative production level that must be achieved before reproductive processes start, then would be possibly that summer deciduous species reach the level before than evergreens. This also would explain the fact that decidous species yield fruit during the first recovery stages after fire, before the evergreens.

Although vegetative recovery of *T. trinervis* is similar to the one present in evergreen species, it does not develop a larger canopy (Araya & Avila 1981, Segura et al. 1993). This is the result of its modular architecture, since the largest proportion of the foliar area are formed by short shoots, which in turn are shedding modules (Hoffmann 1972, Montenegro et al.1989).

During the second growth season after fire flowers were not observed in the burnt shrubs, with the exception of *T. trinervis*. The quick restarting of flowering in this species motivated its classification as a pirogenic species (Montenegro & Teillier 1988). However, our results indicate that flowering is not stimulated after fire; it only reaches levels similar to those found in undisturbed sites (Table 2).

T. trinervis regenerates in burnt sites not only through resprouting, but also through the establishment of new individuals. Although the volume of resprouting is smaller than that reached by other matorral species (Araya & Avila 1981, Segura et al. 1993) *T. trinervis* is one of the species that reach the larger relative cover in the seedling bank established during the spring following fire (Keeley & Johnson 1977, Segura et al. 1993). There is evidence that these plantlets arise from seeds that survived intermediate intensity fire impacts (Muñoz and Fuentes 1989, Segura et al. 1993).

The fact that resprouting shrub species of *T. trinervis* can develop fruit faster than other matorral species is a new indicator that the potentiality of this species to establish new individuals in burnt sites is greater than that of evergreen species and could explain the larger relative cover they reach indegraded sites.

TABLE 2

Mean reproductive and vegetative modules formed in shrubs located in recently burned equatorial slopes and in equatorial slopes wich were relatibely undisturbed during the last ten years. Standard desviation is shown in brackets.

Promedio de los módulos vegetativos y reproductivos formados en arbustos ubicados en laderas ecuatoriales recientemente incendiadas y en laderas ecuatoriales relativamente poco perturbadas desde hace diez años. Entre paréntesis se indican las desviaciones stándard.

Analyzed species	Burnt slope Vegetative modules	Burnt slope Reproductive modules	Control slope Vegetative modules	Control slope Reproductive modules
Q. saponaria	47.6 3.50)	0	5.2(3.15)	0
L. caustica	27.6(7.68)	0	3.6(1.16)	0
T. trinervis	64.4(9.97)	37.6(11.43)	8.2(1.68)	36.2(4.49)

ACKNOWLEDGMENTS

This research was financed in part by Grant FONDECYT 1940655 to G. Montenegro and A. Mellon Foundation.Appreciation is due to Dr. James Mauseth for reading andc ommenting the manuscript. R. Ginocchio was financed by a Fundación Andes doctoral fellowship.

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